

Reprinted from Hare, Jonathan A. and Robert K. Cowen. 1995. Effects of age, growth rate, and ontogeny on the otolith size-fish size relation in bluefish, *Pomatomus saltatrix*, and the implications for back-calculation of size in fish early life history stages. Canadian Journal of Fisheries and Aquatic Sciences 52: 1909-1922, with permission from the National Research Council Canada (NRC-CISTI).

Effect of age, growth rate, and ontogeny on the otolith size – fish size relationship in bluefish, *Pomatomus saltatrix*, and the implications for back-calculation of size in fish early life history stages¹

Jonathan A. Hare and Robert K. Cowen

Abstract: The otolith size – fish size relationship was examined in field-collected larval and pelagic juvenile bluefish, *Pomatomus saltatrix*. The purpose was to evaluate the central assumption of proportional back-calculation techniques, namely that otolith and somatic growth are in constant proportion. Age-independent variability was found between otolith size and fish size that differed between ontogenetic stages. Stage-specific growth rate effects were also identified. Finally, the otolith size – fish size relationship changed at certain ontogenetic stage transitions. These effects, as well as others that have been found, are discussed with regard to the assumption of constant proportionality between otolith growth and fish growth. In light of this discussion, the overall validity of constant proportionality becomes suspect when applied to the early life history stages of fishes. Future work should take a longitudinal approach to the analysis of the relationship between otolith growth and somatic growth. In addition, regression and proportional methods should be modified to account for growth rate and ontogenetic effects. Finally, a relative size approach is presented that is appropriate in situations that require only relative measures of fish size. This relative size approach has several benefits and these are discussed in relation to other back-calculation procedures.

Résumé : Nous avons examiné la relation entre la taille de l'otolithe et la taille du poisson dans des échantillons prélevés sur le terrain de larves et de juvéniles pélagiques de tasserger (*Pomatomus saltatrix*). Notre objectif était d'évaluer l'hypothèse centrale des techniques de rétrocalcul proportionnel, selon laquelle la croissance de l'otolithe et la croissance somatique seraient en proportion constante. Nous avons découvert une variabilité indépendante de l'âge entre la taille de l'otolithe et la taille du poisson, variabilité qui différerait selon le stade ontogénique. Nous avons aussi repéré des effets spécifiques au stade sur le taux de croissance. Enfin, la relation taille de l'otolithe – taille du poisson changeait lors de certaines transitions entre les stades ontogéniques. Ces effets, ainsi que d'autres qui ont été observés, sont analysés par rapport à l'hypothèse de proportionnalité constante entre la croissance de l'otolithe et celle du poisson. À la lumière de cette analyse, la validité globale de la proportionnalité constante suscite des doutes quant à son application aux premiers stades biologiques des poissons. Les travaux futurs devraient adopter une approche longitudinale de l'analyse de la relation entre la croissance de l'otolithe et la croissance somatique. De plus, il faudrait modifier la méthode de régression et la méthode proportionnelle pour tenir compte des effets du taux de croissance et du stade ontogénique. Enfin, nous présentons une approche de la taille relative qui convient aux situations ne nécessitant que des mesures relatives de la taille du poisson. Cette approche présente plusieurs avantages, que nous examinons par rapport aux autres méthodes de rétrocalcul.

[Traduit par la Rédaction]

Received August 24, 1994. Accepted April 12, 1995.
J12553

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Introduction

The study of growth in larval and juvenile fishes has benefited greatly from the finding that increments are formed daily in the otoliths of many species. Daily increments allow the age of an individual to be determined (Brothers et al. 1976; Campana and Neilson 1985; Jones 1986). The incremental nature of otolith growth also provides a record of otolith size-at-age, from which fish size-at-age can be estimated using back-calculation techniques (see reviews by Francis 1990; Campana and Jones 1992). Such estimates of fish size can then be used to examine the role of size and growth in regulating larval fish survival, a topic of long-standing interest (see reviews by Rothschild 1986; Anderson 1988; Leggett and DeBlois 1994).

Back-calculation techniques were initially developed for the estimation of adult fish size from scale annuli, but these techniques have been used to estimate fish size from marks on a variety of other hard parts. Scale proportional techniques assume that if a scale was 10% larger at capture than the average scale of a fish of comparable size, then the individual's scale would be 10% larger than average throughout its life (the body proportional hypothesis is similar but is in terms of body size rather than scale size; see Francis 1990). It is imperative to evaluate this basic back-calculation assumption before the method is applied. Many studies examining otoliths of larval and juvenile fish have concluded that otolith growth and somatic growth are proportional on the basis of significant correlations between measures of otolith and somatic size (the term coupling has been used, but see below). These correlations indicate a general correspondence between otolith size and somatic size, but this would be expected, since the size of any two body parts will be correlated over time simply because they are both growing (Cock 1966; Shea 1985). To demonstrate a linkage between otolith size and fish size, the age-independent variability in the relationship must be assessed. Additionally, many studies have provided evidence counter to the basic assumption that otolith and somatic growth occur in a constant proportion (the term decoupling has been used, but see below). Given the potential utility of the otolith as an individual record of daily size and growth, it is important to examine the factors that might affect the otolith growth – somatic growth relationship with regard to the proportionality assumption of back-calculation. Once this is completed, the various back-calculation techniques available can be evaluated with regard to these findings.

As part of a larger program studying the processes that drive larval survival and subsequent recruitment of bluefish, *Pomatomus saltatrix* (Pisces: Pomatomidae), along the eastern coast of the United States, we are testing the hypothesis that size and growth rate are important components of survival. Accomplishing this specific test is dependent on our ability to compare the sizes of larvae at specific points in their individual histories. Before these size histories can be constructed, the otolith size – fish size relationship must be examined and the various techniques of back-calculation evaluated. The specific goals of this study were threefold. First, the age-independent variability in the otolith size – fish size relationship was examined. Second,

the effects of growth rate and ontogeny on the otolith size – fish size relationship were evaluated in terms of their potential role in affecting the proportionality of otolith growth and somatic growth. Finally, these findings were considered in terms of available back-calculation techniques. The overall intent was to choose an appropriate procedure for back-calculation, one that best accounts for the complexities of the otolith size – fish size relationship.

As stated above, back-calculation assumes that otolith growth and somatic growth are in constant proportion. Studies examining otolith and somatic growth, however, have used the terms coupling and decoupling. In this paper, proportional growth will be used in place of the term coupling. By extension, if otolith growth and somatic growth are not in constant proportion, then this equates with the term decoupling. This terminology will be used because the assumptions of back-calculation are phrased in terms of proportionality. There is also a large body of literature examining the general relationship between the growth of various body parts (see reviews of allometry by Cock 1966; Gould 1966). The continued use of the terms coupling and decoupling to describe the relationship between otolith growth and somatic growth serves only to isolate this specific problem from the more general context of allometry and from the basic assumptions of back-calculation.

Material and methods

Larval collection and otolith procedures

The ichthyoplankton methods used for the collection of young bluefish have been described in detail elsewhere (Hare and Cowen 1991, 1994; Cowen et al. 1993). Bluefish were chosen for otolith analysis to represent the entire size range collected, from 2-mm yolk-sac larvae to 25-mm pelagic juveniles. Standard lengths of all individuals ($n = 112$) were measured to the nearest 0.01 mm using an ocular micrometer. Body depth and caudal peduncle depth were also measured to the nearest 0.01 mm with an ocular micrometer from a subset of individuals ($n = 60$) as part of another study (see Hare and Cowen 1994). From the measurements of length, body depth, and caudal peduncle depth, body area was calculated assuming a simplified fish shape (Fig. 1).

Both sagittal and lapillar otoliths were removed from all individuals for determination of age and otolith size. The otoliths to be used in this study were selected on the basis of an initial evaluation of otolith clarity. Otoliths were examined at 400 \times magnification on at least three separate occasions in random order with the aid of an image analysis system. Each examination included enumeration of the number of daily increments and measurement of the maximum otolith radius. Nyman and Conover (1988) determined that sagittal increments are formed daily in estuarine juvenile bluefish and Hare and Cowen (1994) argued that sagittal increments are also formed daily in larval and pelagic juvenile bluefish. Whether increment formation in the lapillus is daily has been questioned for preflexion larvae (Hare and Cowen 1994), and thus age was estimated by calculating the mean number of sagittal increments for each individual. Likewise, maximum otolith radius was estimated by calculating the mean value from each examination of an individual otolith.

The ontogenetic stage of each individual was determined on the basis of otolith characters previously described (Hare and Cowen 1994). Hare and Cowen (1994) found that (i) the first otolith increment forms at hatching, (ii) there is an apparent change in the increment deposition rate of the lapillus associated with flexion, and (iii) secondary growth centers begin to form at the transition from larva to juvenile. On the basis of these findings, individuals with two or fewer sagittal increments were classified as yolk-sac larvae ($n = 32$). Individuals with a lapillus/sagitta increment ratio > 1.75 were classified as preflexion larvae ($n = 24$) (see Fig. 2). If the lapillus/sagitta ratio was ≤ 1.75 , individuals were classified as postflexion ($n = 38$) (see Fig. 2). Individuals with secondary growth centers present on their sagitta were termed posttransformation pelagic juveniles ($n = 18$).

Statistical background and analyses

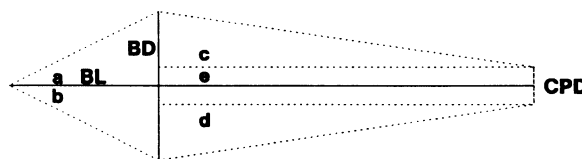
The basic approach used to examine the age-independent variability in the otolith size – fish size relationship was to model otolith size and fish size with regard to age. The residuals of these models were then used to quantify the amount of age-independent variability. A fish with a positive fish size-on-age residual represents a fish that is large for its age. A fish with a positive otolith size-on-age residual represents a fish with a large otolith for its age. If there is no age-independent variability in the otolith size – fish size relationship, then the residuals of the two models (otolith size-on-age and fish size-on-age) should be perfectly correlated (Fig. 3A). By extension, a decreasing correlation between otolith size-on-age and fish size-on-age residuals equates to increasing age-independent variability.

Two factors that may affect the proportionality of otolith and somatic growth were examined: growth rate effects and ontogenetic effects. To examine growth rate effects, an approach similar to the analysis of age-independent variability was used. Otolith size and fish age were modeled with regard to fish size. A fast-growing fish will have a negative residual; it will be young for its size. If fast-growing fish have smaller otoliths, then the residuals of age-on-fish size and otolith size-on-fish size will be positively correlated (Fig. 3B), thereby demonstrating a growth rate effect on the otolith size – fish size relationship.

The effect of ontogeny on the otolith size – fish size relationship was examined using two approaches. First, age-independent variability and growth rate effects were analyzed for specific ontogenetic stages. The results of these analyses were then compared to determine if there were ontogenetic differences. Second, the slopes of the otolith size – fish size relationship for the various ontogenetic stages were compared. If the slopes are significantly different, then otolith growth is not in constant proportion with somatic growth (Cock 1966).

To conduct the analysis of residuals, several different relationships were modeled: fish size-on-age and otolith size-on-age (for the analysis of age-independent variability), as well as age-on-fish size and otolith size-on-fish size (for the analysis of growth rate effects). Both sagittae and lapilli were examined to test whether the results of the various analyses differed between otoliths. In addition, two measures of fish size were used to test whether the

Fig. 1. Schematic of method by which body area of young bluefish was calculated. A simplified fish shape was used where BD is body depth (mm), BL is body length (mm), and CPD is caudal peduncle depth (mm).



$$\text{Body Area} = a + b + c + d + e$$

where:

$$a = b = 0.5(0.3BL)(0.5BD)$$

$$c = d = 0.5(0.7BL)(0.5BD - 0.5CPD)$$

$$e = CPD(0.7BL)$$

measure of body size affected the age-independent variability in the otolith size – fish size relationship. Length was measured in all individuals and body area was calculated from a subset of larvae. Thus, a total of seven combinations of variables were modeled for the analyses of residuals: length-on-age, body area-on-age, sagittal radius-on-age, lapillar radius-on-age, age-on-length, sagittal radius-on-length, and lapillar radius-on-length.

The analyses were conducted in several steps. (i) Since a residual as a measure of an individual's departure from the population is dependent on the model used, a variety of models were fit to the various relationships (e.g., length-on-age). (ii) The best model for a given relationship was then chosen on the basis of several criteria. (iii) Residuals from the best models in terms of age were analyzed to determine the age-independent variability in the otolith size – fish size relationship. (iv) Residuals from the best models in terms of length were analyzed to determine the effect of growth rate on the otolith size – fish size relationship. (v) Ontogenetic effects were evaluated by testing for differences between stages in age-independent variability and growth rate effects, and the slopes of the otolith size – fish size relationship were compared between the different ontogenetic stages.

Explaining these steps in more detail, the first step applied first- through fourth-order polynomial models to each of the seven combinations of variables. Campana and Jones (1992) have discussed the use of linear and curvilinear functions for modeling fish growth. It is important to note that these models are used solely to develop the best fit for the seven combinations of variables from which the residuals will be used in the analysis of age-independent variability and of growth rate and ontogenetic effects. Each of the seven combinations of variables was modeled using the following eight equations:

$$y = a + bx \quad \text{model 1}$$

$$y = a + bx + cx^2 \quad \text{model 2}$$

$$y = a + bx + cx^2 + dx^3 \quad \text{model 3}$$

$$y = a + bx + cx^2 + dx^3 + ex^4 \quad \text{model 4}$$

$$\ln(y) = a + bx \quad \text{model 5}$$

$$\ln(y) = a + bx + cx^2 \quad \text{model 6}$$

$$\ln(y) = a + bx + cx^2 + dx^3 \quad \text{model 7}$$

$$\ln(y) = a + bx + cx^2 + dx^3 + ex^4 \quad \text{model 8}$$

Fig. 2. Schematic representation of method by which pre- and post-flexion larvae were distinguished on the basis of lapillar and sagittal increment number. Figurative data are the lapillar increment number for three illustrative individuals, with the ratio of sagittal to lapillar increments given in parentheses. Hare and Cowen (1994) found an apparent change in the increment formation rate of the lapillus at flexion from one increment every other day to one increment every day. Given this pattern, the relative number of sagittal to lapillar increments defines individuals as pre- or post-flexion. Increment at hatching is designated number 0, so that sagittal increment number represents age. Yolk adsorption occurs at about 2 days (Hare and Cowen 1994). The ratio of sagittal and lapillar increments decreasing to 1.75 is indicative of the change in increment deposition rate and thus the occurrence of flexion.

	Sagittal Increment Number															Individual
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
Lapillar Increments	1 (2.00)	2 (2.00)	3 (2.00)	4 (2.00)	5 (2.00)	6 (2.00)	7 (1.85)	8 (1.75)	9 (1.67)							1
	1 (2.00)	2 (2.00)	3 (2.00)	4 (2.00)	5 (2.00)	6 (1.83)	7 (1.71)	8 (1.63)	9 (1.56)	10 (1.50)						2
	1 (2.00)	2 (2.00)	3 (2.00)	4 (2.00)	5 (1.80)	6 (1.67)	7 (1.57)	8 (1.50)	9 (1.44)	10 (1.40)	11 (1.36)					3
Ontogenetic Stage	Yolk-Sac Larvae		Pre-Flexion Larvae					Post-Flexion Larvae								

where y is the dependent variable; x is the independent variable; and a , b , c , d , and e are constants of a given model. Models were fit to the data using the multiple general linear hypotheses module of SYSTAT (Wilkinson 1990).

The second step determined which of the eight models best fit each of the combination of variables. This determination was based on several criteria common to linear regression analyses. Specifically, the residuals of the model must be normally distributed, they must have a constant variance with respect to the independent variable, and they must be independent of each other. In addition, all data in the relationship must be described by the same model, and the model must explain a significant amount of the relationship's variation. These conditions were evaluated for each model, and then the model with the fewest parameters, which best satisfied these criteria, was used to calculate the residuals of a given relationship for further analysis. Normality of a model's residuals was tested using a Kolmogorov-Smirnov test ($\alpha = 0.05$). Constant variance and independence of a model's residuals were evaluated visually by plotting residuals versus predicted values. Whether all values of a given relationship were adequately described by the model was quantified by counting the number of residuals with Cook's distance values >0.5 . Cook's distance measures the influence of each observation on the model's coefficients. A large Cook value means that if that observation were removed, the coefficients of the model would change substantially. The F statistic and r^2 value were used as relative measures of the significance of a given model. All tests and analyses were performed using SYSTAT and are described in Wilkinson (1990).

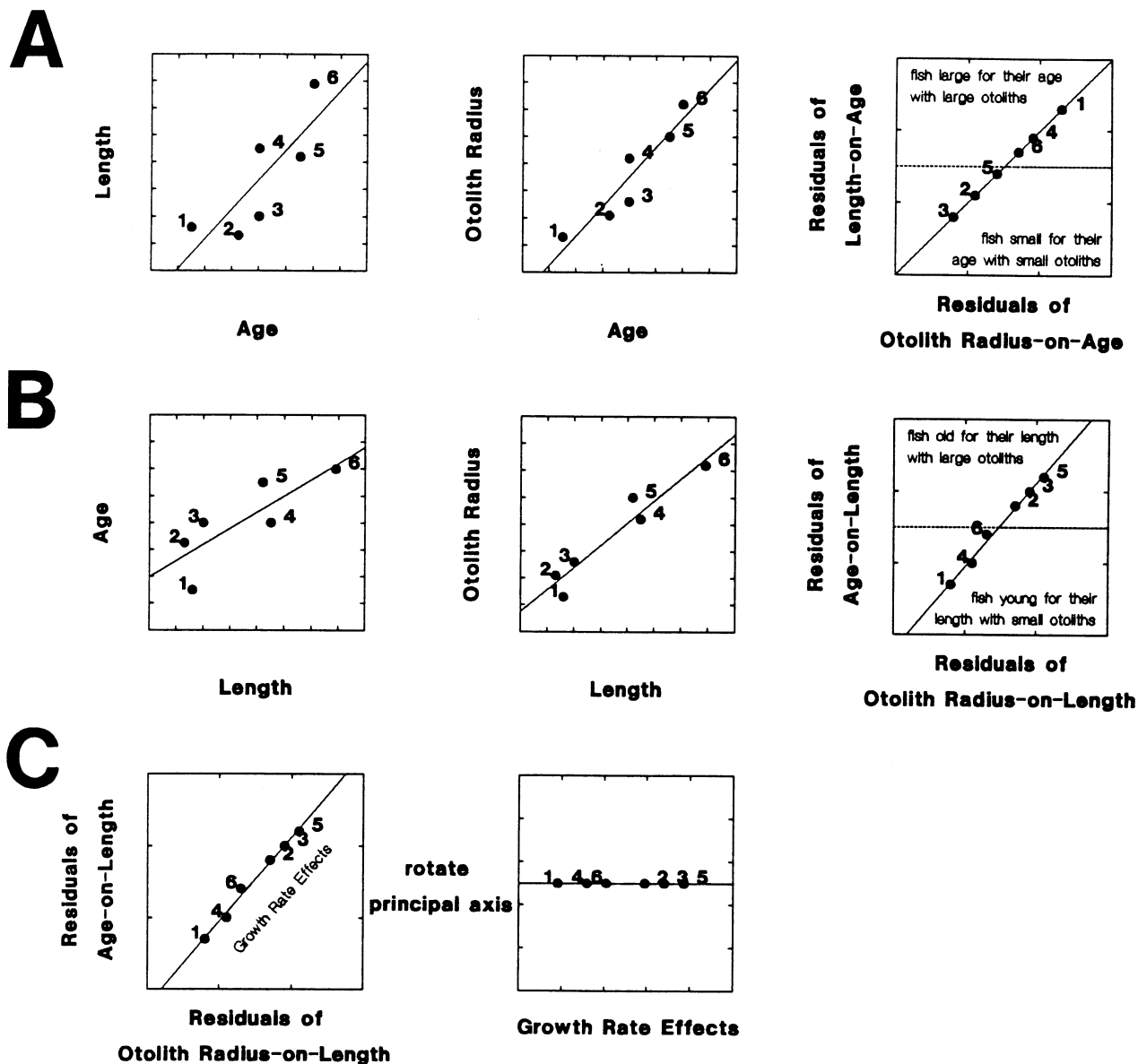
Once a model was chosen for each relationship, the third step examined the age-independent variability in the

relationship between otolith size and fish size. Pearson correlation coefficients (Sokal and Rohlf 1981) were calculated of the residuals from the otolith size-on-age models and the body size-on-age models. Differences between the measure of body size and otolith size were then evaluated using a test of homogeneity among correlation coefficients outlined in Sokal and Rohlf (1981) with a significance level of $\alpha = 0.05$. The amount of age-independent variability is the amount of variability in the body size-on-age residuals that is not explained by otolith size-on-age residuals.

The fourth step analyzed the effect of growth rate on the otolith size – fish size relationship. Pearson correlation coefficients were calculated of the otolith radius-on-length models and the age-on-length model residuals. Growth rate effects were then quantified through an analysis of the principal axes (see Sokal and Rohlf 1981) of the otolith radius-on-length residuals and the age-on-length residuals. The principal axis in this case represented the axis of slower growing fish with larger otoliths and faster growing fish with smaller otoliths. The residuals were rotated so that the principal axis became the x axis. In this orientation, the x value represents the degree to which an individual's otolith size was affected by differences in growth rate (Fig. 3C). This estimate of growth rate effects was then used in a multiple regression model with the residuals of otolith size-on-age to determine how much variability in the body size-on-age residuals could be explained, effectively accounting for age and growth rate effects on the otolith size – fish size relationship. The multiple general linear hypotheses module of SYSTAT (Wilkinson 1990) was used.

The first part of the final step repeated the above analyses for the different ontogenetic stages: yolk-sac, larvae,

Fig. 3. Schematic of the predictions that (A) fish larvae large for their age will have large otoliths for their age (to determine age-independent variability) and (B) fish larvae old for their length will have large otoliths for their length (to determine growth rate effects), and (C) method by which growth rate effects were quantified.

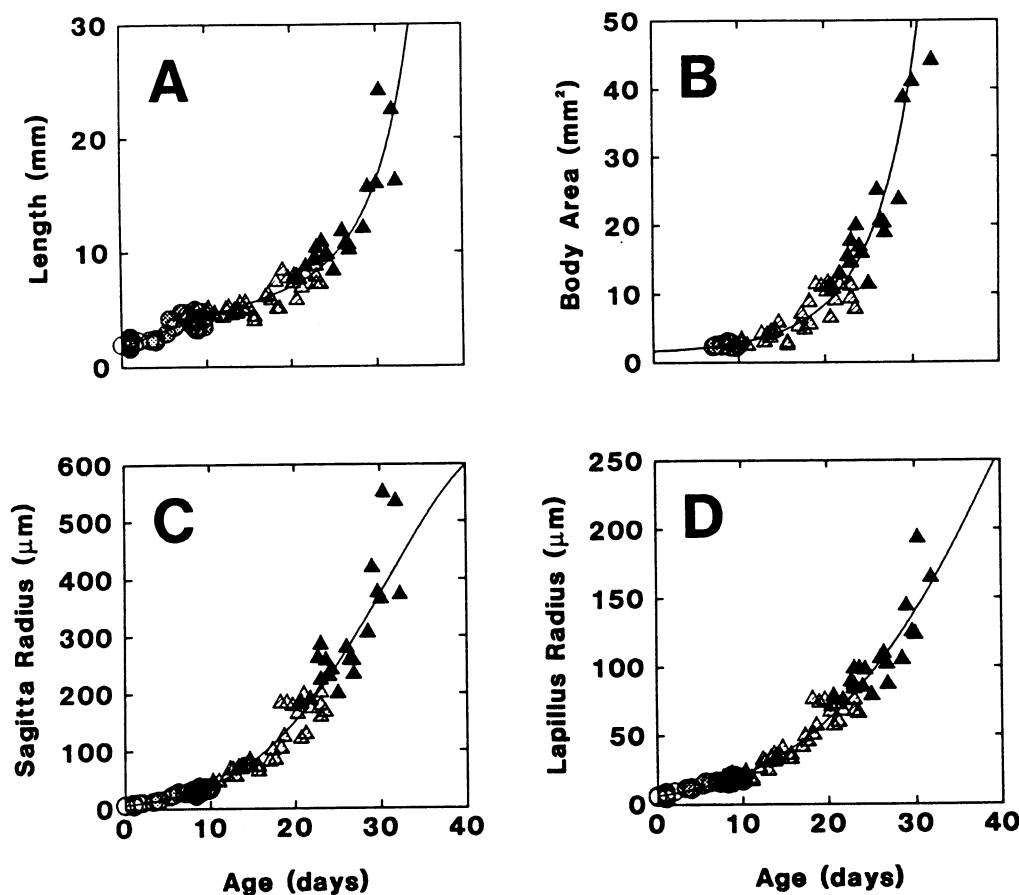


preflexion larvae, postflexion larvae, and pelagic juveniles. Pearson correlation coefficients were calculated for the relationship between otolith size-on-age residuals and length-on-age residuals for each ontogenetic stage (the analysis of age-independent variability). Pearson correlation coefficients were also calculated for each ontogenetic stage for the relationship between otolith radius-on-length residuals and age-on-length residuals (the analysis of growth rate effects). Comparisons of stage-specific correlation coefficients were made using a pairwise test of homogeneity among two coefficients (Sokal and Rohlf 1981). Since all comparisons were made, a Bonferroni correction was used to determine the level of significance; for each analysis, six comparisons were made resulting in a Bonferroni significance level of $\alpha = 0.008$ (Wilkinson 1990). The multiple

regression, which included the rotated axis of the growth rate effect, was also repeated for each ontogenetic stage. Multiple correlation coefficients (r values) derived from the model of each ontogenetic stage were then compared with the multiple correlation coefficient derived from the model that included all stages (from above) using the test of homogeneity among correlation coefficients (Sokal and Rohlf 1981). Since specific tests were planned (model r value of each stage to model r value of all stages), a Bonferroni correction was not used and significance was tested at $\alpha = 0.05$.

The final portion of the fifth step calculated the slope of the otolith size – fish size relationship for each ontogenetic stage. The equation of simple allometry was used, $y = ax^k$, where the log transformation results in $\log(y) = \log(a) +$

Fig. 4. Data and best-fit models for (A) length-on-age, (B) body area-on-age, (C) sagittal radius-on-age, and (D) lapillar radius-on-age relationships for young bluefish. Ontogenetic stages are distinguished by different symbols: open circles are yolk-sac larvae, hatched circles are preflexion larvae, hatched triangles are postflexion larvae, and solid triangles are pelagic juveniles.



$k\log(x)$ (Gould 1966). If otolith and somatic growth are in constant proportion throughout the ontogeny of bluefish, then the slope (k) should not be different between ontogenetic stages. All slopes were compared using an unplanned comparison of a set of regression coefficients (Sokal and Rohlf 1981).

Results

Model choice

Otolith size-on-age relationships and body size-on-age relationships were described best by second- and third-order natural log-transformed models, respectively. For length-on-age, the third-order natural log transformed model was chosen (model 7; Fig. 4A), because of the independence of its residuals and the higher r^2 value compared with the first- and second-order models. The second-order natural log transformed model was chosen for the body area-on-age relationship (model 6; Fig. 4B), because of the independence and constant variance of the residuals and the higher r^2 value. The second-order natural log transformed model was also chosen for sagittal radius-on-age and lapillar radius-on-age relationships (model 6; Figs. 4C and 4D). In the case of sagittal radius-on-age, this model was chosen

because of the independence of the residuals and the higher F statistic and r^2 value; in the case of lapillar radius, this model was chosen because of the normality and independence of the residuals, as well as the higher r^2 value.

Third-order models were chosen for the age-on-length and otolith radius-on-length relationships. The nontransformed third-order model was chosen for the age-on-length relationship (model 3; Fig. 5A), because of independence of the residuals and Cook's distance values. However, the natural log transformed third-order model was chosen for both the sagittal radius-on-length and lapillar radius-on-length relationships (model 7; Figs. 5B and 5C), because of the normality and independence of residuals and higher F statistic and r^2 values.

Age-independent variability

Analysis of otolith size-on-age and body size-on-age residuals demonstrated that there is variability in the otolith size – fish size relationship when the effect of age is removed. Pearson correlation coefficients for length and otolith radius residuals were 0.639 ($p < 0.001$) and 0.593 ($p < 0.001$) for the sagitta and lapillus, respectively (Figs. 6A and 6B). Pearson correlation coefficients for body area and otolith radius residuals were 0.840 ($p < 0.001$) and 0.722 ($p < 0.001$)

for the sagitta and lapillus, respectively (Figs. 6C and 6D). The correlation coefficient for the sagittal radius – body area residuals was significantly greater than the coefficient for the sagittal radius – body length residuals ($t_s = 2.853$, $p < 0.01$), while the coefficients for the lapillar radius – body area and lapillar radius – body length residuals were not significantly different ($t_s = 1.411$, $p > 0.05$).

Growth rate effects

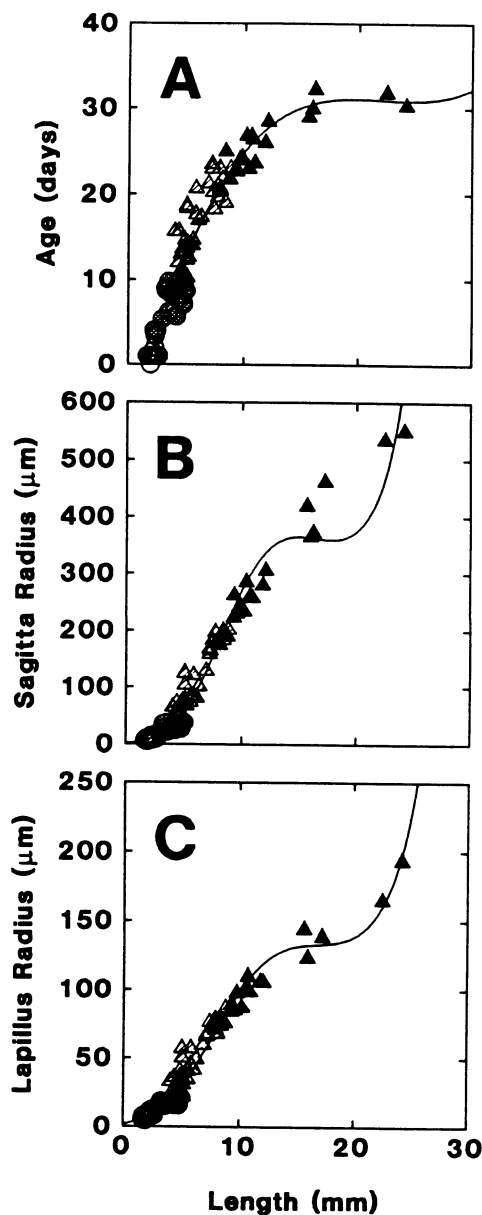
Comparison of the residuals of age-on-length with the residuals of otolith radius-on-length demonstrated that there was a significant effect of growth rate on the otolith size – fish size relationship. Pearson correlation coefficients were 0.807 ($p < 0.001$) and 0.770 ($p < 0.001$) for the sagitta and lapillus, respectively (Figs. 7A and 7B). When the rotated principal axes of these relationships (i.e., the measure of the effect of growth rate) were included in a multiple regression model with the residuals of otolith radius-on-age, a significant amount of the variation in the length-on-age residuals was explained ($r^2 = 0.800$ and 0.830, for sagitta and lapillus, respectively, $p < 0.001$ for both otoliths). Thus, if growth rate effects are accounted for, much of the age-independent variation in fish size can be explained by otolith size.

Ontogenetic effects

The stage-specific analysis of age-independent variability found differences between ontogenetic stages. Age-independent variability decreased from the preflexion stage to the pelagic juvenile stage (Table 1). With regard to sagittal radius and length, there was a significantly greater correlation between otolith size-on-age and length-on-age residuals in the postflexion stage than in the preflexion stage ($t_s = 3.438$, $p < 0.001$, Bonferroni correction $\alpha = 0.008$). In terms of lapillar radius and length, there was a significantly greater correlation between otolith size-on-age and length-on-age residuals in the pelagic juvenile stage than in the preflexion stage ($t_s = 3.085$, $p < 0.008$, Bonferroni correction $\alpha = 0.008$) and the postflexion stage ($t_s = 2.822$, $p < 0.008$, Bonferroni correction $\alpha = 0.008$). Other comparisons were not significant.

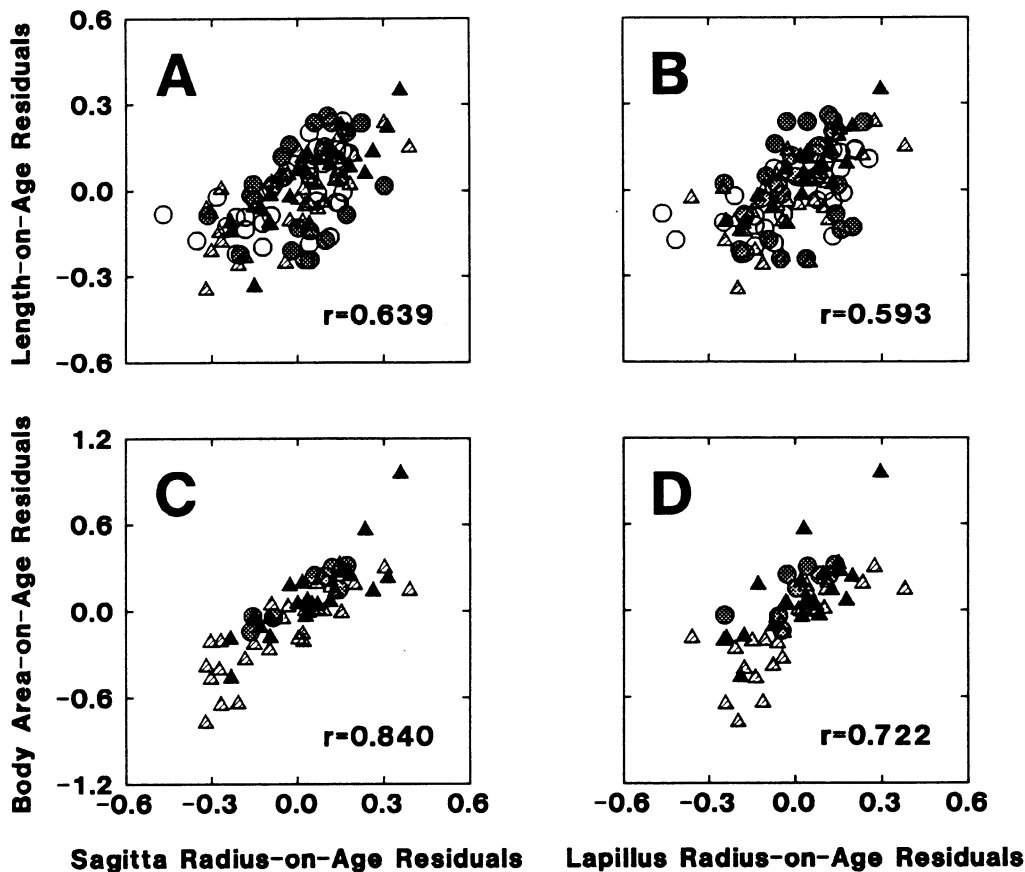
Ontogenetic differences were also found in the effect of growth rate on the otolith size – fish size relationship (Table 1). With regard to the sagitta, growth rate effects were significantly lower in pelagic juveniles than in preflexion larvae ($t_s = 4.060$, $p < 0.001$, Bonferroni correction $\alpha = 0.008$) and postflexion larvae ($t_s = 3.673$, $p < 0.001$, Bonferroni correction $\alpha = 0.008$). Growth rate effects were significantly higher in preflexion larvae than in yolk-sac larvae ($t_s = 3.240$, $p < 0.001$, Bonferroni correction $\alpha = 0.008$) and postflexion larvae ($t_s = 2.941$, $p < 0.008$, Bonferroni correction $\alpha = 0.008$) (Table 1). In terms of the lapillus, growth rate effects were significantly lower in both yolk-sac larvae and pelagic juveniles than in preflexion larvae ($t_s = 3.965$, $p < 0.001$ and $t_s = 3.192$, $p < 0.001$, respectively, Bonferroni correction $\alpha = 0.008$) and postflexion larvae ($t_s = 3.510$, $p < 0.001$ and $t_s = 3.320$, $p < 0.001$, respectively, Bonferroni correction $\alpha = 0.008$). Other comparisons were not significant. Thus, decreases in the effect of growth rate coincide with decreases in the amount of age-independent variability in the otolith size – fish size relationship (Fig. 8A).

Fig. 5. Data and best-fit models for (A) age-on-length, (B) sagittal radius-on-length, and (C) lapillar radius-on-length relationships for young bluefish. Ontogenetic stages are represented as in Fig. 4.



When growth rate effects (the rotated principal axis of otolith radius-on-length residuals and age-on-length residuals; see Fig. 3C) were incorporated into stage-specific multiple regression models with the residuals of otolith radius-on-age, more of the variability in length-on-age residuals was explained compared with the models that combined all ontogenetic stages (Table 2). Multiple correlation coefficients for the yolk-sac and postflexion larvae were significantly greater than those of the general models for both otoliths. In addition, the explanatory power of these multivariate models apparently decreased during development, suggesting an increase in the variability of the otolith size – fish size relationship that is not due to age differences or growth rate effects (Fig. 8B).

Fig. 6. Correlation analysis of residuals evaluating amount of age-independent variability in the otolith size – fish size relationship of young bluefish: (A) length versus sagittal radius residuals, (B) length versus lapillar radius residuals, (C) body area versus sagittal radius residuals, and (D) body area versus lapillar radius residuals. The greater the correlation, the less the age-independent variability (see Fig. 3A). Ontogenetic stages are represented as in Fig. 4.



Ontogenetic differences were also found between the stage-specific slopes of the simple allometric approximation of the otolith size – fish size relationship (Fig. 9). For the sagitta, the slope for the postflexion stage was significantly greater than that of the other three stages (difference = 1.187, $p < 0.001$; 1.112, $p < 0.001$; 1.096, $p < 0.001$ for yolk-sac larvae, preflexion larvae, and pelagic juveniles, respectively). Other comparisons were not significant. Similarly, for the lapillus, the slope for the postflexion stage was significantly greater than that for the other three stages (difference = 0.801, $p < 0.05$; 1.224, $p < 0.001$; 1.018, $p < 0.001$; for yolk-sac larvae, preflexion larvae, and pelagic juveniles, respectively). Other comparisons were not significant.

Discussion

Proportionality of the otolith size – fish size relationship

The results of this study demonstrate that there is age-independent variability in the otolith size – fish size relationship (Fig. 6) and that this variability is stage specific (Fig. 8A). The analyses of the effect of growth rate revealed that much of the age-independent variation could be accounted for by differences in growth rate, but again this was shown

to be stage specific (Fig. 8A). If ontogenetic effects and growth rate effects were both accounted for, then a greater amount of the variability in fish size could be explained (Table 2), but unexplained variability increased ontogenetically (Fig. 8B). Since it is characteristic for young fish to have variable growth rates and to undergo ontogenetic stage transitions, a back-calculation technique should be used that can account for both growth rate and ontogenetic effects on the otolith size – fish size relationship. However, before back-calculation methods are considered, the factors that may affect the proportionality of otolith growth and somatic growth must be discussed in more detail.

There are several factors that may affect the otolith size – fish size relationship, as well as the relationship between otolith growth and somatic growth. One factor identified in this study is the measure of somatic size used. Many studies base their acceptance or rejection of proportionality between otolith growth and somatic growth on a correlation between otolith size and fish size. In this study, less age-independent variability was found between body area and otolith radius than between length and otolith radius. Thus, in a given study, the measure of body size used may not be the measure that is most closely correlated

Table 1. Pearson correlation coefficients calculated for length-on-age residuals and otolith radius-on-age residuals (analysis of age-independent variability) and for age-on-length residuals and otolith radius-on-length residuals (analysis of growth rate effects) for each ontogenetic stage.

Ontogenetic stage	Correlations between residuals of length-on-age and otolith radius-on-age		Correlations between residuals of age-on-length and otolith radius-on-length	
	Sagittal radius	Lapillar radius	Sagittal radius	Lapillar radius
Yolk-sac larvae	0.632***	0.663***	0.627***	0.264***
Preflexion larvae	0.340	0.330	0.931***	0.887***
Postflexion larvae	0.733***	0.611***	0.824***	0.818***
Pelagic juveniles	0.876***	0.919***	0.034	0.124

*** $p < 0.001$.

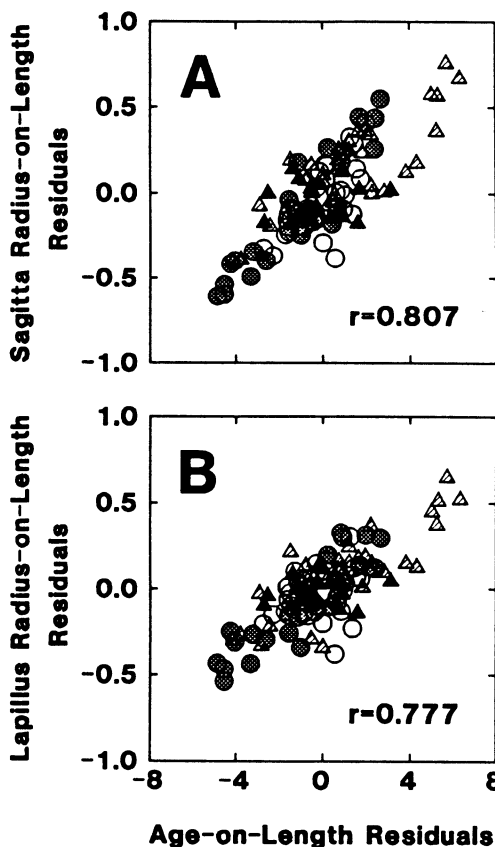
with otolith size. Although this measurement effect is not a true biological factor, it must be recognized prior to drawing conclusions on the basis of the correlation between otolith size and fish size.

Temperature, on the other hand, may biologically affect the relationship between otolith and somatic growth. Mosegaard et al. (1988) found that otolith growth responded differently to temperature than somatic growth; at temperatures beyond those typically encountered by the organism (hyperoptimal), somatic growth decreased while otolith growth increased. These results demonstrate that the proportionality between otolith and somatic growth may be temperature dependent and, therefore, not constant.

Another factor that may affect the relationship between otolith growth and somatic growth is differences in the response time of somatic and otolith growth to changes in the environment. Molony and Choat (1990) were able to distinguish somatic size differences in experimental populations prior to recognizing otolith size differences and they concluded that there is a lag in the response of otolith growth compared with somatic growth. Gutiérrez and Morales-Nin (1986) found that increment width and temperature were cross-correlated with lags of 0–7 d, suggesting that otolith growth is lagged from changes in temperature, which by extension could create changes in somatic growth. Thus, otolith growth and somatic growth may respond to changes in the environment (e.g., ration level, temperature) at different rates, indicating that during such periods, the relationship between otolith growth and somatic growth cannot remain constant.

In addition to differences in response time, a variety of studies have shown that otolith growth continues during periods of no somatic growth, as well as during periods of somatic loss (Marshall and Parker 1982; Volk et al. 1984; Eckmann and Rey 1987; Maillet and Checkley 1990; Sogard 1991). These observations indicate that there is some minimal rate of otolith growth, which is independent of somatic growth. Secor and Dean (1989) argued that

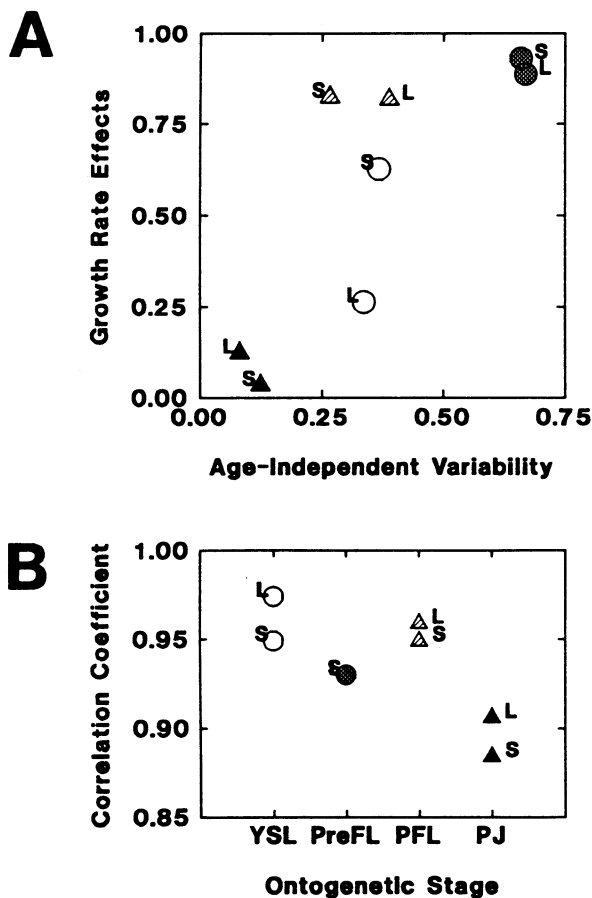
Fig. 7. Correlation analysis of residuals evaluating the occurrence of growth rate effects in the otolith size – fish size relationship of young bluefish: (A) sagittal radius versus age residuals and (B) lapillar radius versus age residuals. The greater the correlation, the greater the effect of growth rate (Fig. 3B). Ontogenetic stages are represented as in Fig. 4.



otolith growth continues during periods of no somatic growth because of the incremental nature of otolith increment deposition. Positive minimal otolith growth during periods when somatic size is not increasing or is decreasing implies that there is not a simple proportional relationship between otolith growth and somatic growth (i.e., the relationship is not $dO/dA = i(dL/dA)$, where O is otolith radius, L is fish length, A is age, and i is a coefficient of proportionality).

The relationship between otolith growth and somatic growth is also affected by the absolute growth rate. Many studies have found that faster growing fish have smaller otoliths at a given length than slower growing fish (i.e., a growth rate effect on the otolith size – fish size relationship) (e.g., Templeman and Squires 1956; Reznick et al. 1989; Secor and Dean 1989; Hovenkamp 1990; Wright et al. 1990; Francis et al. 1993; the present study). If an individual's growth rate relative to the population's average growth rate does not change, then the assumption of proportionality is not violated (Campana 1990). For example, in the simple linear case, the assumption of scale proportional back-calculation (i.e., if a scale were 10% larger at capture than the average scale of a fish of comparable size, then the scale would be 10% larger than average throughout

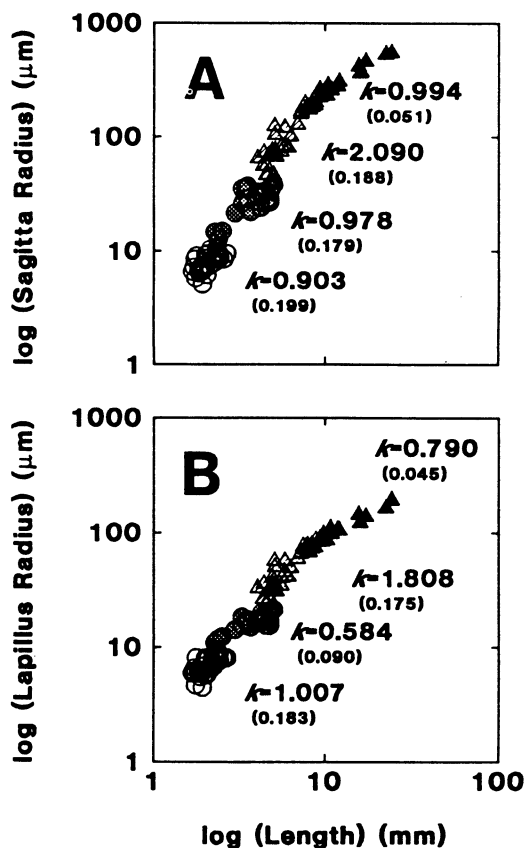
Fig. 8. (A) Correlation coefficients from the analyses of age-independent variability and growth rate effects. Age-independent variability was estimated by subtracting the correlation coefficient of length-on-age and otolith size-on-age residuals from 1 (see Figs. 3A and 6). Growth rate effects were estimated by using the correlation between otolith size-on-length and age-on-length residuals (see Figs. 3B and 7). Comparisons for both sagitta and lapillus are distinguished by S and L, respectively. Ontogenetic stages are represented as in Fig. 4. (B) Correlation coefficients of the multiple regression models for both otoliths (distinguished by S and L as above) and each ontogenetic stage (x axis): yolk-sac larvae (YSL), preflexion larvae (PreFL), postflexion larvae (PFL), and pelagic juveniles (PJ).



the life of the fish) can be interpreted as a growth rate effect; a slower growing fish will have a larger scale at a given length than a faster growing fish. Campana (1990) demonstrated, however, that as the effect of growth rate increases (i.e., slower growing fish have increasingly larger otoliths at a given size), the potential for back-calculation error increases. Also, if an individual's growth rate relative to the population's growth rate changes (e.g., as observed in salmon fry by Wilson and Larkin 1982), then the assumption of constant proportionality will be violated.

Finally, there are two types of ontogenetic influences that may affect the relationship between otolith growth and somatic growth. This study found that the age-independent

Fig. 9. Simple allometric plot of the (A) sagittal radius-length and (B) lapillar radius-length relationship for young bluefish. Slopes of the equation $\log(\text{otolith radius}) = \log(b) + k\log(\text{length})$ for each ontogenetic stage are provided, and the standard error of the slopes are in parentheses. Ontogenetic stages are represented as in Fig. 4.



variability in the otolith size – fish size relationship and the effect of growth rate on this relationship differed between ontogenetic stages (Fig. 8). The sources of these differences remain unclear, yet this finding implies that the accuracy of any back-calculation procedure may be stage specific.

A second ontogenetic effect is the occurrence of stage-specific otolith growth – somatic growth relationships (Campana 1984; Rice et al. 1985; Cowen 1991; Toole et al. 1993; Hare and Cowen 1994; the present study). Campana (1990) modeled an ontogenetic change in growth rates using size to determine the timing of a life history transition and found that his biological intercept procedure (a modified proportional technique) back-calculated fish sizes accurately. Laidig et al. (1991) used a curvilinear proportional technique to back-calculate fish size, with inflection points in essence representing ontogenetic changes in the otolith size – somatic size relationship. Life history stage transitions, however, occur at variable size and age (Chambers and Leggett 1987, 1992; Cowen 1991; McCormick 1994; Sponaugle and Cowen 1994) and thus ontogenetic changes will result in a complex relationship between otolith size and fish size. More importantly, these changes imply that the relationship between otolith growth and somatic growth is not constant through life history

stage transitions (Fig. 9), thereby violating the assumptions of proportional back-calculation.

It is clear that many factors affect the relationship between otolith growth and fish growth and that additional research is necessary to elucidate this relationship. This study involved a cross-sectional analysis of the otolith size – fish size relationship for field-collected bluefish larvae and pelagic juveniles (i.e., one set of measurements per individual with individuals representing different ages and ontogenetic stages; see Cock 1966). Other studies have performed cross-sectional analyses on controlled populations (e.g., Secor and Dean 1989, 1992). To further our understanding of the functional relationship between otolith growth and somatic growth, longitudinal studies are necessary. The size of individuals must be tracked over time and this individual record of size must be compared with the size record contained within the individual's otolith (see Cock 1966). Several studies have followed individuals over time (e.g., Wilson and Larkin 1982), and these should be used as a foundation for more involved work. A multivariate approach should be used to estimate fish size and otolith size, since the first component in a multigroup principal components analysis can be a consistent measure of general size (Strauss and Fuiman 1985; Lombarte and Leonart 1993). Treatments should examine the different factors that affect the otolith growth – somatic growth relationship: temperature, growth rate, response lags, and ontogenetic transitions. Such a set of experiments would allow a comprehensive analysis of the functional relationship between otolith and fish growth and a thorough evaluation of the appropriateness of the various back-calculation procedures.

This study, however, provides evidence that a basic assumption of proportional back-calculation may be violated in the early life history stages of fishes. Ontogenetic changes in the relationship between otolith size and somatic size imply that there are ontogenetic changes in the relationship between otolith growth and somatic growth (see Cock 1966; Gould 1966; Laird et al. 1968; Shea 1985). In addition, if individual growth rates change relative to the population's growth rate, then as a result of growth rate effects, the proportionality between otolith growth and somatic growth must necessarily change (see Campana 1990). This study indicates, however, that if growth rate effects and ontogenetic effects can be accounted for in back-calculation, then much of the variability in the otolith size – fish size relationship can be explained (Table 2).

Back-calculation and fish early life history stages

Two potential approaches exist by which growth and ontogenetic effects can be incorporated into existing back-calculation procedures for the estimation of size in the early life history stages of fishes. The first is to use stage-specific multiple regression of otolith size and fish age to estimate fish size. The idea that age be included in a regression back-calculation formula to account for growth rate effects was suggested by Secor and Dean (1992). Ontogenetic effects would be accounted for by using a different multiple regression model for each ontogenetic stage. The second approach is to modify Campana's (1990) biological-intercept procedure and use stage-specific otolith growth – somatic growth relationships to incorporate ontogenetic

Table 2. Multiple correlation coefficients for multiple regression models (length-on-age residuals = constant + otolith radius-on-age residuals + principal axis of growth rate effects).

Ontogenetic stage	Sagittal radius		Lapillar radius	
	<i>r</i>	<i>t_s</i>	<i>r</i>	<i>t_s</i>
All stages	0.894	—	0.911	—
Yolk-sac larvae	0.949	−3.951***	0.974	−3.024***
Preflexion larvae	0.930	−0.908	0.930	−0.525
Postflexion larvae	0.949	−1.959*	0.959	−2.063
Pelagic juveniles	0.884	0.180	0.906	0.102

Note: The *t_s* values are provided for comparisons between stage-specific models and the model for all ontogenetic stages.

**p* < 0.05.

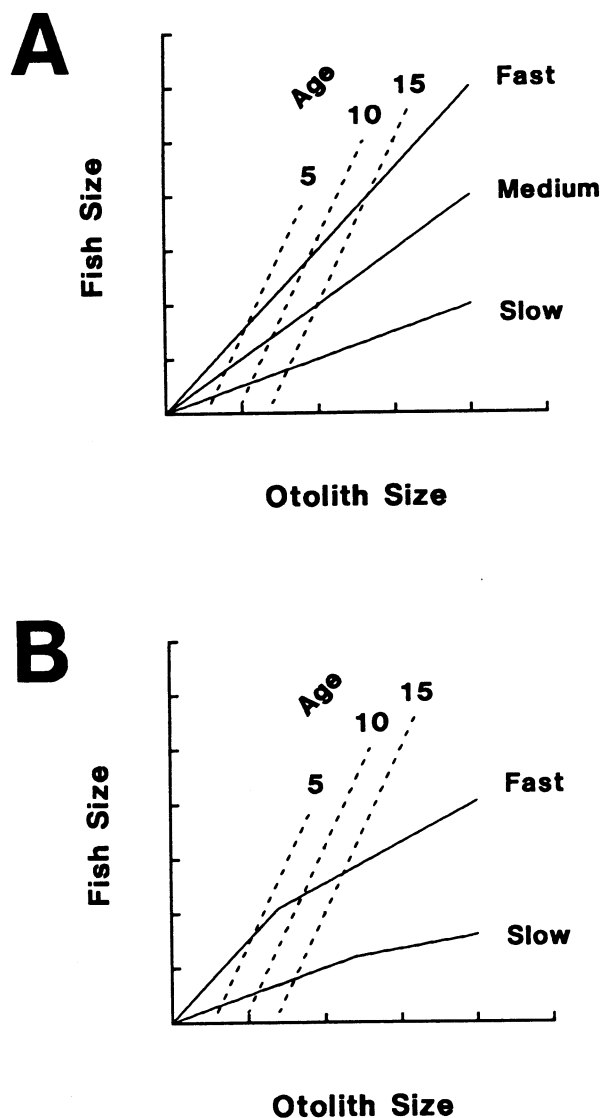
****p* < 0.001.

effects. Age could also be incorporated to correct for growth rate effects. This model would be similar to Campana's (1990) eq. 7, which used a series of daily growth increments to compensate for time-varying growth rates. Both of these approaches would require that the timing of ontogenetic transitions be determined from the otolith record (see Hare and Cowen 1994), so that the correct regression or otolith growth – somatic growth proportion could be applied to an otolith size in a given ontogenetic stage. It is important to note that incorporating these changes does not deal with temperature-derived effects and response time effects on the otolith growth – somatic growth relationship.

The use of regression techniques versus proportional techniques is a topic of ongoing debate. Secor and Dean (1992) have advanced the use of regression techniques, while Francis (1990) and Campana (1990) have advanced the use of proportional techniques. Within proportional techniques, there is also a debate as to which regression should be used to estimate the parameters of the average fish (see Francis 1990; Ricker 1992) and this argument extends to other uses of linear regression (Ricker 1973; Laws and Archie 1981; Campana and Jones 1992). This study and the above discussion indicate that the basic assumption of proportional techniques may be violated by growth rate effects and by ontogenetic effects in the early life history stages of fishes. Clearly, caution should be used in the application of current back-calculation procedures to larval and juvenile fishes. In the future, longitudinal studies should be able to isolate and quantify the effects of temperature, response times, growth rate, and ontogeny on the relationship between otolith growth and somatic growth. Changes in the current back-calculation techniques, such as using a stage-specific multiple regression or a stage-specific biological intercept procedure, can then be considered in light of these new data, thereby further refining the ability to numerically estimate fish size from otolith size.

Not all back-calculation, however, requires the actual estimation of fish size from otolith size. Some questions are comparative and simply require calculating the relative fish size-at-age (see parallel approach presented by Hoenig et al. 1990). Formally stated, this relative size approach assumes that at a specific age, a larva with a larger otolith

Fig. 10. (A) Schematic of relative size approach of estimating relative fish size-at-age from otolith size-at-age. (B) Schematic showing that approach is not necessarily influenced by ontogenetic changes in the relationship between otolith growth and somatic growth (transition indicated by change in slope).



also has a larger body size. This statement is supported by this study and by many others (e.g., Wilson and Larkin 1982; Volk et al. 1984; Eckmann and Rey 1987; Alhossaini and Pitcher 1988; Hovenkamp 1990; Maillet and Checkley 1990; Sogard 1991; Bradford and Geen 1992; Tzeng and Yu 1992; Zhang and Runham 1992). Such a relative size approach solves the problem of growth rate effects because age is used to standardize the comparison of otolith size (Secor and Dean 1992; Fig. 10A). In addition, this method determines relative body size, so that ontogenetic stage-specific functions are not necessary to estimate actual fish size, nor is it necessary to determine the timing of life history stage transitions from the otolith record.

As discussed above, there are other factors that can influence the otolith size – fish size relationship. By comparing

sizes at a specific age within a specific ontogenetic stage, stage-specific otolith growth – somatic growth relationships will not influence the relative comparisons (Fig. 10B). However, the error in such comparisons will in part be dependent on ontogenetic stage as indicated by the stage-specific differences in age-independent variability (Table 1) and by differences in the amount of variability explained by accounting for growth rate effects (Fig. 8). Response lags and temperature-mediated effects cannot be accounted for using this method and will create uncertainty, but these remain general problems common to all back-calculation. The strength of this approach is that it does not require the actual calculation of fish size, thereby removing assumptions about the specific procedures used to model the otolith size – fish size relationship. In addition, the analyses presented above allow the error in the relative size technique to be estimated for different ontogenetic stages and ages, and thus conclusions based on this technique can be evaluated with regard to this error. Finally, this method is both conceptually and practically simpler than other methods.

The relative size approach has benefits for a certain subset of back-calculation purposes, namely comparative questions. By determining the otolith size-at-age distribution of survivors (see Methot 1983; Rice et al. 1987; Crecco and Savoy 1987) and comparing this with the otolith size-at-age distribution of the larval population as a whole, the importance of size to survival can be assessed. Likewise, by comparing distributions of increment widths (e.g., the width between increment 5 and 10), patterns in survival relative to age-specific growth can be examined. However, this approach is not applicable to all comparative questions. For example, it can be used for intracohort comparisons, but for intercohort comparisons, it must first be determined that the otolith size – fish size relationship is the same among cohorts (see Secor and Dean 1989). Additionally, factors that vary both with size and age cannot be examined because of the influence of growth rate effects. For example, size-at-metamorphosis cannot be studied with the relative size approach because there is also variation in age-at-metamorphosis (Chambers and Leggett 1987, 1992; Cowen 1991; McCormick 1994; Sponaugle and Cowen 1994). Further refinements in back-calculation, such as those suggested above, are necessary before factors that confound age and size can be examined.

Back-calculation techniques provide a useful tool for the examination of the role of size and growth in the survival of larval fishes. In instances where actual numerical estimation of larval size is required, current back-calculation techniques should be used with caution because growth rate variation and ontogenetic stage transitions are characteristic of the early life history stages of fishes. The relative size approach, however, should provide a powerful method by which a variety of size- and growth-related hypotheses can be tested, thereby contributing to our understanding of the processes that create variation in larval fish survival.

Acknowledgments

Various drafts of the manuscript benefited from the comments of Jim Churchill, Dave Conover, Art Kendall, Steve

Morgan, Eric Schultz, and Su Sponaugle. Thoughtful reviews were provided by Steve Campana, Chris Francis, and an anonymous reviewer. This last reviewer suggested that we go to the allometry literature and we thank them for that contribution. We also thank Steve Campana and John Dean, the organizers of the International Otolith Symposium, and their sponsors, contributors, and donors for providing fellowship money to J.A.H. to attend the meeting. This paper is a result of research funded in part by the New York Department of Environmental Conservation through the Dingell-Johnson Federal Aid in Sport-Fish Restoration, by the Hudson River Foundation through their doctoral fellowship program, by the American Fishing Tackle Manufacturers Association through their Andrew J. Boehm Fellowship Award, by the Sounds Conservancy through their Marine Conservation, Education and Research for the Marine Region of Southern New England granting program, and by the National Oceanic and Atmospheric Administration (NOAA) (awards NA86AA-D-SG045 and NA90AA-D-SG078 to the Research Foundation of the State University of New York for the New York Sea Grant Institute). The views expressed herein are those of the authors and do not necessarily reflect the views of NOAA or any of its subagencies.

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